
Syringantha coulteri (Hooker f.) T. McDowell, a New Combination,
and Remarks on the Relationships of the Monotypic Mexican
Genus *Syringantha* Standley (Rubiaceae)

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ABSTRACT. *Exostema coulteri* Hooker f. is transferred to the monotypic genus *Syringantha* Standley, and the new combination *Syringantha coulteri* (Hooker f.) T. McDowell is made. Analysis of leaf, flower, fruit, and pollen characters indicates the affinities of *Syringantha* are with the tribe Hamelieae. A description, illustrations, and micrographs of pollen and leaves of *S. coulteri* (Hooker f.) T. McDowell are provided.

HISTORY OF SYRINGANTHA

Exostema coulteri Hooker f. was first published by W. B. Hemsley (1879), who attributed the species to J. D. Hooker based on a manuscript in the Kew herbarium. The specific epithet honors Thomas Coulter (1793–1846), an Irish botanist and curator of the herbarium of Trinity College, Dublin, whose collections from central Mexico include the type for *E. coulteri*. The assignment of this species to the genus *Exostema* (Persoon) Bonpland is not discussed in the published description, but evidently was based on characters of the corolla, stamens, capsule, and seeds. In particular, a more or less tubular corolla, basifixed linear anthers with filaments inserted near the base of the corolla tube, and a septicidally dehiscent bilocular capsule with winged seeds are characters shared with the genus *Exostema*. However, the fully exerted stamens, for which *Exostema* was named, are lacking in *E. coulteri*, which has the stamens only partially exerted.

Standley (1921) maintained *E. coulteri* in his treatment of *Exostema* for the North American Flora, but noted "description compiled," and apparently did not see any specimens of this species. In the dichotomous key to the 26 species of *Exostema* included in Standley's treatment, *E. coulteri* is the only one with "Stamens included; corolla lobes short, rounded."

In 1930 Standley described the monotypic genus *Syringantha* Standley with one species, *Syringantha loranthoides* Standley, based on Mexican collections by Karwinsky on loan from the Leningrad

Botanical Garden herbarium. Standley stated, "*Syringantha* is evidently a close relative of *Exostema* . . . but the corollas are conspicuously different," noting that the short, broad and erect corolla lobes of *Syringantha* contrast with the long, narrow and recurved lobes in *Exostema*. He overlooked *Syringantha*'s resemblance to the anomalous *Exostema* species *E. coulteri*.

Lorence recognized that *Syringantha loranthoides* is identical to *Exostema coulteri* and used the earlier name *E. coulteri* Hooker f. in his annotations of specimens and in a checklist of Mexican genera of the Rubiaceae (Lorence, 1990). This reduction of *S. loranthoides* to *E. coulteri* has been followed in a recent review of Rubiaceae classification by Robbrecht (1994).

In the course of a revision of the genus *Exostema* I have examined the morphology and pollen structure of *E. coulteri* and other *Exostema* species and have determined that *E. coulteri* should be excluded from *Exostema*. Differences between *Syringantha* and *Exostema* are summarized in Table 1. The synapomorphies for *Exostema*—the corolla with a narrowly cylindrical tube, ligulate recurved corolla lobes, and the anthers long exerted—are lacking in *Syringantha* (Fig. 1). *Syringantha* also lacks characters common to the genera closest to *Exostema*, notably *Coutarea* Aublet and *Portlandia* P. Browne (Andersson & Persson, 1991; Bremer, 1992), which include anthers with latrorse dehiscence and tricolporate pollen with spinulose, foveolate exine (Fig. 2). *Exostema* and closely related genera lack several characters of *Syringantha*, such as caducous stipules, a subconical nectar disc, and apiculate stamen connectives. Moreover, *Syringantha* has abundant raphide bundles in stems, leaves, flowers and fruits (Fig. 3), which have not been previously reported and are absent from all *Exostema* species (pers. obs.). Consequently, the monotypic genus *Syringantha* is here maintained, and the new combination *Syringantha coulteri* (Hooker f.) T. McDowell is made for this species.

Table 1. Comparison of selected characters of *Syringantha*, *Hamelia*, and *Exostema*.

Character	<i>Syringantha</i> , <i>Hamelia</i>	<i>Exostema</i>
Raphides	present	absent
Stipule persistence	caducous	persistent
Inflorescence branching	upper axes monochasial, secundiflorous	upper axes usually dichasial, never secundiflorous
Corolla color	bright yellow, orange or deep red	white turning pink, cream, tan or pale yellow
Stamen filament shape	flattened	terete-filiform
Anther dehiscence	introrse	latrorse
Connective shape	apiculate	not apiculate
Nectariferous disc shape	subconical	discoid
Funicular attachment on seed	at center of seed body	at edge of seed body
Pollen exine type	smooth, reticulate	spinulose, foveolate

RELATIONSHIPS OF *SYRINGANTHA*

Tribal affiliation of *Syringantha* is problematic. Traditional subfamilies and tribes have been based on a few characters, such as fruit type (Schumann, 1891) or presence of raphides (Bremekamp, 1966), and have been artificial groups. Because they have capsules and winged seeds, *Syringantha* and *Exostema* historically have been included in the tribe Cinchoneae (Robbrecht, 1988). Recent authors have allied *Exostema* and *Syringantha* with the tribe Condamineae (Andersson & Persson, 1991), and with a group of genera "associated with *Portlandia*" to be segregated from that tribe (Robbrecht, 1993), but have not evaluated *Syringantha* in detail. Raphides are presumably absent from these tribes, although exceptions to this pattern have been noted for certain genera (Robbrecht, 1988; Taylor, 1992). The combination of winged seeds, raphides, and imbricate corolla aestivation in *Syringantha* is incompatible with the subfamily and tribal groupings currently recognized (Robbrecht, 1988).

Syringantha may be closely related to the genus *Hamelia* Jacquin, a neotropical group of shrubs with fleshy fruits and many small wingless seeds. Despite the obvious difference in fruit and seed types, *Syringantha* and *Hamelia* share many vegetative, floral, and fruit traits. Both have raphides and deciduous stipules. Both have secundiflorous inflorescence axes and bright yellow corollas (also orange or red in *Hamelia*) with short, imbricate lobes. The subcylindrical, somewhat angular corolla shape in *Syringantha* resembles several *Hamelia* species. In both *Syringantha* and *Hamelia* there is a large, subconical ovarian disc that persists as a conspicuous extension of the fruit above the calyx limbs. In all *Hamelia* species the connective of the stamen is extended beyond the anthers into a short

tip (Elias, 1976). *Syringantha* also has an apiculate connective. Pollen in *Hamelia* is similar to *Syringantha* pollen in type and size (Fig. 2). Finally, the restricted range of *Syringantha* in eastern Mexico falls within the wider neotropical distribution of *Hamelia* (Elias, 1976).

The tribe Hamelieae Kunth has been investigated in a cladistic study by Bremer (1987), who defined it as a monophyletic group of five neotropical genera. Lorence and Dwyer (1988) supported Bremer's circumscription of the tribe, but added two small Mexican genera (*Eizia* Standley and *Plocanophyllon* T. S. Brandege). The Hamelieae, which Bremer and Lorence consider a well supported natural group, is variable for characters such as fruit type (capsule or berry), corolla aestivation (imbricate or contorted), and pollen exine sculpting (smooth reticulate or spinulose foveolate) (Bremer, 1987; Lorence & Dwyer, 1988). Characters for the tribe as summarized by Robbrecht (1988) include raphides present, usually terminal inflorescences with flowers often yellow, and stamens inserted near corolla base, although these traits also occur in various tribes in the Rubioideae. Synapomorphies for the Hamelieae, according to Bremer (1987), include granulate or tuberculate exotestal cells, inflorescence bracts scale-like or lacking, and aestivation imbricate or right-contorted. Lorence and Dwyer (1988) emphasized the importance of capsule dehiscence, which they described as initially loculicidal, to distinguish the dry-fruited genera of the tribe. The microstructure of the exotestal cell tangential walls of *Syringantha* has not been examined. *Syringantha* is consistent with the bract, inflorescence, and dehiscence character states for the Hamelieae.

The inclusion of *Syringantha* in the tribe Hamelieae would add winged seeds to this already

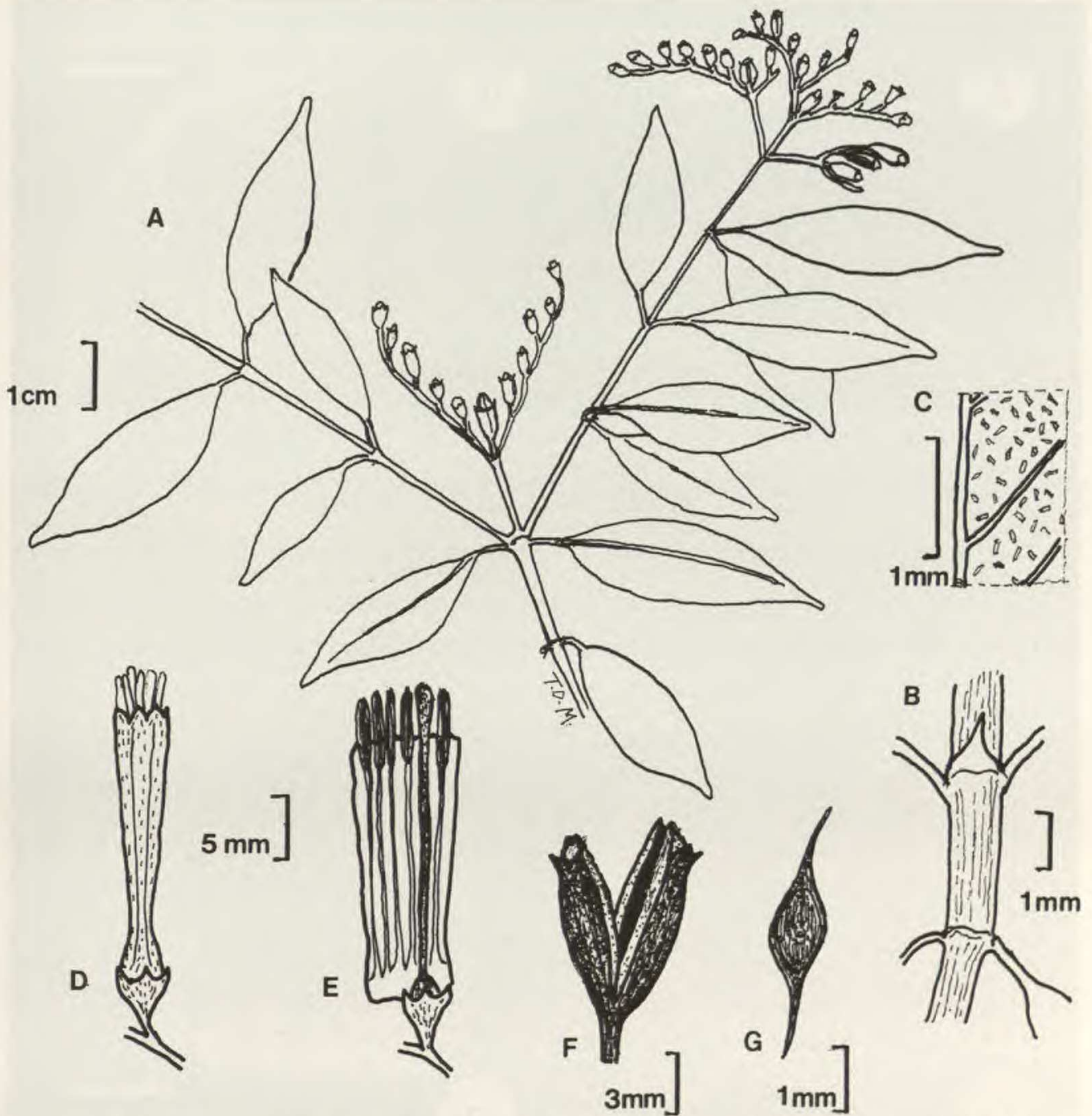


Figure 1. *Syringantha coulteri* (Hooker f.) T. McDowell. —A. Habit. —B. Node, stipule caducous. —C. Raphides in young leaf blade. —D. Flower. —E. Opened flower. —F. Dehiscent capsule. —G. Seed. (A, C, Stanford et al. 2207; B, D, Webster & Armbruster 20526; E, Diaz Barriga 3872; F, G, Hernández M. & Rodríguez 4967.)

diverse tribe. Bremekamp (1966) argued that winged seeds of different morphologies had arisen in various lineages, and that the character "winged seeds" was therefore unsuitable for defining a natural group. Recent analyses of Rubiaceae phylogeny have confirmed this conclusion (Bremer & Eriksson, 1992). Bremekamp (1952) transferred several genera with winged seeds from the Cinchoneae to the Hedyotideae, emphasizing the greater importance of characters such as raphides and exotestal cell pitting. A similar, albeit controversial, realignment of winged-seeded genera from the tribe Cinchoneae to a tribe of fleshy-fruited genera has

been proposed by Bremer (1992), who transferred *Exostema* and allied genera to the tribe Chiococceae on the basis of morphological and chloroplast DNA characters.

The traditional, artificial subdivision of the Rubiaceae according to a few simple characters continues to confuse perceptions of phylogenetic relationships and character evolution within this large family. It has long been acknowledged that groups based on the characters of ovules per locule (one vs. many) and fruit type (dry vs. fleshy) do not represent evolutionary lineages (Verdcourt, 1958; Bremekamp, 1966). If the pluriovulate locule is prim-

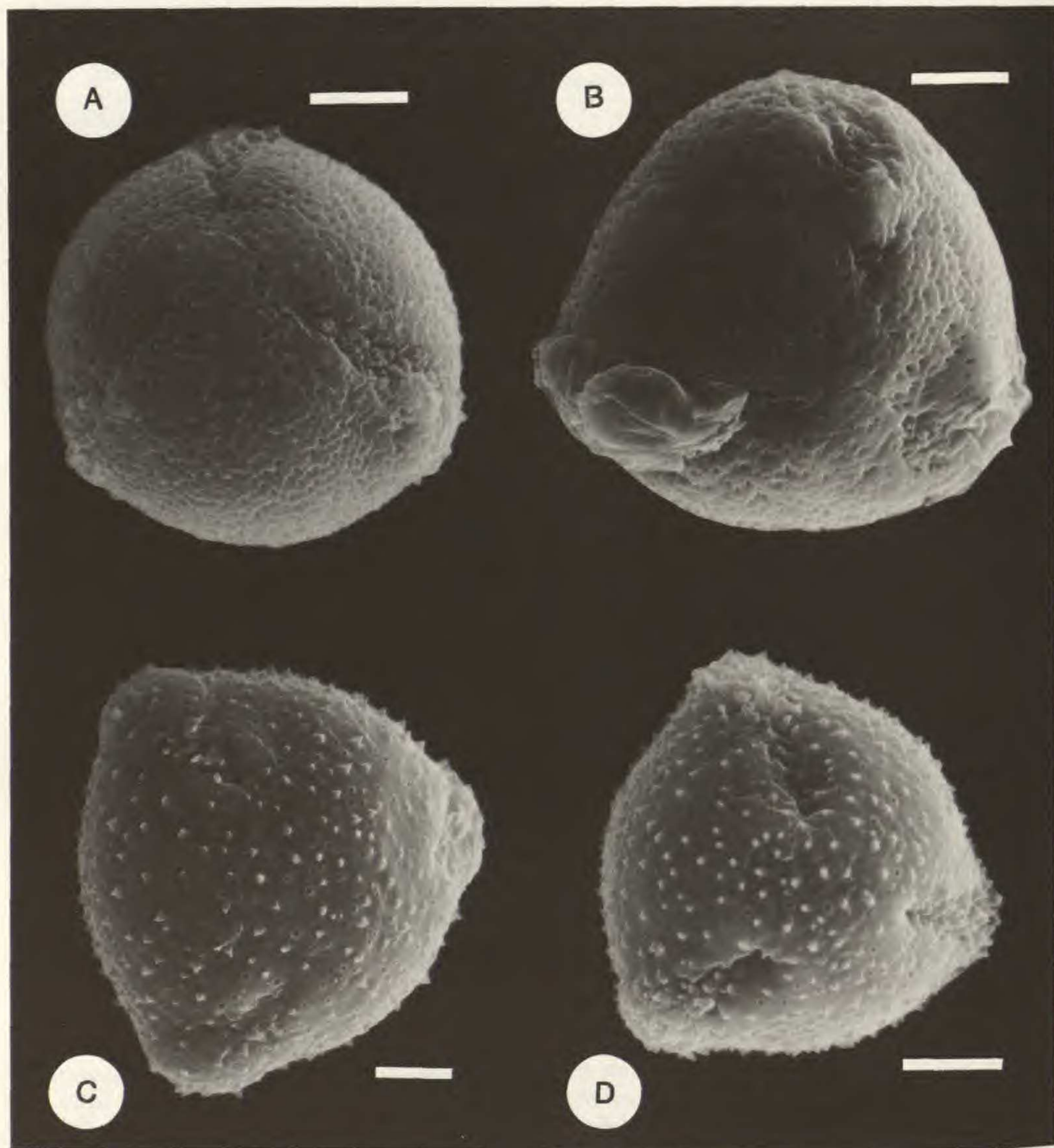


Figure 2. Pollen in scanning electron microscopy, polar view. —A. *Syringantha coulteri*. —B. *Hamelia patens* Jacquin. —C. *Exostema caribaeum* (Jacquin) Roemer & Schultes. —D. *Exostema mexicanum* A. Gray. Scale bars = 5 μm . (A, Weaver 2116; B, C, Taylor 1383; C, T. McDowell 5009; D, Steyermark 51128.)

itive in the Rubiaceae, and the fleshy fruit has been multiply derived, then a natural classification of the family will need to recognize a number of subfamilies or tribes in which diverse fruit types occur (Bremer & Eriksson, 1992). Similarly, if raphides evolved more than once in the family, their occurrence marks two or more lineages, and may be expected in various subfamilial taxa (Robbrecht, 1988; Taylor, 1992). For many taxa in the Rubiaceae, morphological characters such as ra-

phide occurrence and pollen type have yet to be examined (Robbrecht, 1988). The investigation of molecular characters, such as chloroplast DNA restriction site studies (Bremer & Jansen, 1991) and DNA sequences (Bremer et al., 1995; Natali et al., 1995) is now under way for many Rubiaceae taxa. As additional morphological and molecular data are assembled and analyzed, evolutionary patterns in the Rubiaceae will be clarified. It seems likely that current concepts of subfamilial relationships and

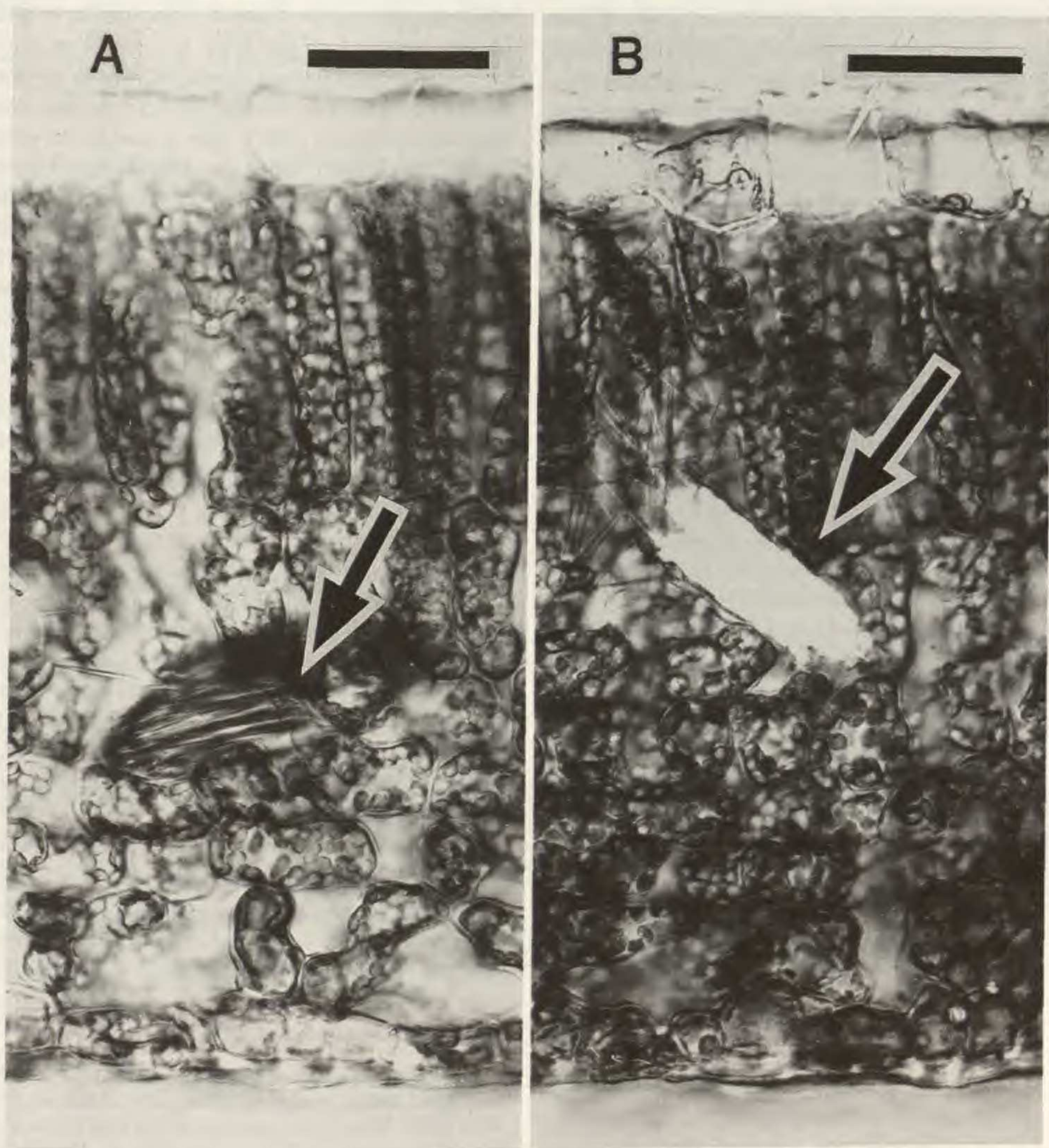


Figure 3. Transverse section of leaf of *Syringantha coulteri*, with raphide bundles indicated by arrows. —A. With one polarizing filter, needle crystals visible within and beside bundle. —B. With paired polarizing filters, raphide bundle birefringent. Scale bars = 50 μm . (A, B, *Lorence 5043*.)

character evolution in the Rubiaceae will change markedly as a natural system of classification develops.

TAXONOMY

Syringantha coulteri (Hooker f.) T. McDowell, comb. nov. Basionym: *Exostema coulteri* Hooker f., in Hemsley, *Diagn. Pl. Nov. Mexic.*: 32. 1879. TYPE: Mexico. Hidalgo: Zimapán, *Coulter 209* (holotype, K; isotype, MO).

Syringantha loranthoides Standley, *Field Mus. Nat. Hist., Bot. Ser.* 8(3): 153. 1930. TYPE: Mexico. Entre San

Diego y la Hacienda de Santiaguillo, July 1842, *Karwinsky 308*, upper specimen (lectotype, selected here, LE; isolectotypes, MW, F-fragment).

Shrub 0.7–3.5 m high, with abundant raphides throughout, leafy branches 1–2 mm thick, terete to slightly flattened (obtusely tetragonal), young twigs puberulent-glabrescent, red-brown, bark dark gray or brown, smooth or furrowed (not fissured), sometimes with large, irregular lenticels; *stipules* 0.5–1(–2) mm long, triangular to subulate with thickening at base, glabrous, deciduous. *Leaves* with petioles 3–10 mm long, ca. 0.5 mm thick, canaliculate and puberulent to glabrescent, *leaf blades*

2.5–8 cm long, 0.4–2.2 cm wide, narrowly elliptic to lanceolate, base cuneate, apex briefly acuminate with tip rounded, chartaceous to subcoriaceous, surface finely bullate, margin often revolute, drying green to yellow-green, glabrous or slightly puberulent along midrib above, glabrous beneath (midrib and blade not recurved), midrib slightly raised and narrowly canaliculate above, slightly prominent beneath, lateral veins 3–6 per side, obscure or evident but not prominent, venation visible to 3° veins, domatia lacking, raphides visible in immature leaves. *Inflorescence* terminal, 3–6 cm high, 3–5 cm wide, a compound cyme with primary branching dichasial and lateral branches secundiflorous, main peduncles 1–2 cm long; *flowers* ca. 2 cm long, with pedicels 0.5–2 mm long, ca. 0.3 mm thick, bracteoles minute, linear, to 1 mm long; hypanthium 2–2.5 mm long, to 2.5 mm wide at top, tapering to base, glabrous, calyx lobes 0.5–1.5 mm long, triangular (rarely digitate); *corolla* bright yellow, glabrous, tube 14–20 mm long, 1.5–2.5 mm wide, subcylindrical, expanded at base and constricted above base, lobes 0.5–1.5 mm long, triangular, closing upon anthers and not recurved, raphides visible in corolla; *stamens* partially exerted, filaments flattened, conviviant (forming false tube) toward base, glabrous, inserted about 2 mm above the base of corolla tube, anthers 4–5 mm long, basifixed, dehiscence introrse by longitudinal slits, connective covering anthers abaxially and briefly apiculate, tip ca. 0.5 mm long; style subequal to stamens, narrowly clavate, with stigmatic surfaces linear; *capsule* 5–8 mm long, ca. 3 mm wide, ellipsoid, smooth or with fine costa, not lenticellate, brown, placentae elongate, axile and attached at center of septum, seeds ca. 12 per locule, attachment peltate near center of seed body with acuminate wings overlapping adjacent seeds; *seeds* 3–4 mm long, 0.5–1 mm wide including wing, brown, with elongate acuminate wings at each end of seed.

Phenology. Flowering from April to October (especially in June and July). Fruits persistent through much of year.

Distribution. Mexico, Sierra de Madre Oriental: States of Tamaulipas, Querétaro, and Hidalgo (San Luis de Potosí?). A plant of sclerophyllous thorn scrub (matorral) vegetation on rocky limestone slopes with thin soil, from 1000 to 2000 m elevation. The type locality for *Syringantha loranthoides* Standley, cited as between San Diego and Santiaguillo, is uncertain. No municipality or state was given in Standley's 1930 publication. A search of maps shows many villages in Mexico with those names. A likely placement for that locality, in the

southeast part of the State of Guanajuato, is about 13 km northeast of the town of Acambaro, where there is a village named Santiaguillo with a village named Plaza de San Diego just 5 km to the northeast (Bartholomew, 1989). This would be an extension of the known range for specimens of *Syringantha* into an adjacent region. The Gray Herbarium Index lists the locality for *Syringantha loranthoides* as Chiapas, Mexico. This is far removed from the known range for this species, and is likely a misinterpretation of the original publication due to the occurrence of another village named Santiaguillo in that state.

The type material cited by Standley for *Syringantha loranthoides* includes four separate collections by Karwinsky, numbered 308, 308, 308b, and 308c, from the St. Petersburg (Leningrad) herbarium (LE). The collection dates and/or localities differ for each of these specimens. The lectotype is here designated as Karwinsky 308, upper specimen on sheet. "Type specimen" is written in Standley's handwriting beside this specimen, and its inflorescence bears many flowers. The additional Karwinsky collections are of the same entity, and also bear flowering material. There is a duplicate of the lectotype in Moscow (MW) and a fragment from it in the Field Museum (F).

Syringantha coulteri is a low xeric shrub with bright yellow flowers, corolla tube constricted near base, and corolla lobes overlapping opening of tube, and with linear stamens semi-exserted. Raphides are visible in corolla, fruit, and immature leaves. Seeds are small, brown, and waferlike, with wings acuminate at distal ends.

Additional specimens examined. MEXICO. **Hidalgo:** Municipio Jacala, rocky mountain side, 1250 m, Chase 7333 (MO); Municipio Cardonal, 45 km E of Ixmiquilpan, base of Barrancas de Tolantongo, 1400 m, Hernandez & Rodriguez 4967 (MEXU, MO); 10 km NW of Zimapán, 1000 m, González Medrano 2369 (F, MEXU); 1/2 km N of Molanguito, González Medrano 12789 (MEXU); Municipio Cardonal, Barranca de Tolantongo, Hiriart & Ortiz 43 (MO); Santiaguillo, July 1842, Karwinsky 308—lower specimen (LE, F-fragment); El Pantario et in Santiaguillo, Apr. 1843, Karwinsky 308b (LE, MW, F-fragment); Santiaguillo, Oct. 1842, Karwinsky 308c (LE; F-fragment); 2–2.5 km NE Molanguito, 1950 m, Lorence 5043 (MEXU); Lorence 5044 (F, MEXU); NE of Jacala along highway, km 275–276, 1450 m, Moore & Woods 3676, (CM, GH, US); 11.2 m S of Jacala on Highway 85, 1850 m, Weaver 2116 (MO). **Querétaro:** 8 km NE of La Lagunita, along the highway to Xilitla, 1400 m, Diaz Barriga 3872 (MEXU); Municipio Matamoros, La Vuelta, 18 km NE of Landa de Matamoros, 1500 m, Hernández & Tenorio 7184 (MEXU); 25 km NE of Landa, along road to El Lobo, 1350 m, Rzedowski 9295 (MEXU). **Tamaulipas:** 4 km W of El Capulin, 25 km N of Tula, near turnoff to Bustamante, 1700 m, González Medrano 13191 (MO, MEXU); 4 km SE of Bustamante toward La Presita and Tula, 23°25'N,

99°45'W, 1600 m, *Johnston et al.* 11173 (MEXU, MO); 5 km S of Hoja Verde, *Stanford et al.* 2207 (US); Jaucave, *Viereck* 365 (US); 5 mi. NE of Palmillas, 23°22'N, 99°30'W, 1180 m, *Webster & Armbruster* 20526 (MO). Mexico, no locality: *Coulter* 227 (K), *Coulter* 410 (K).

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Literature Cited

- Andersson, L. & C. Persson. 1991. Circumscription of the tribe Cinchoneae (Rubiaceae)—A cladistic approach. *Pl. Syst. Evol.* 178: 65–94.
- Bartholomew, J. C. 1989. *The Times Atlas of the World*, 9th ed., John Bartholomew and Son, London.
- Bremekamp, C. E. B. 1952. The African species of *Oldenlandia* L. sensu Hiern et K. Schumann. *Verh. Kon. Ned. Akad. Weterisch., Afd. Natuurk., Tweede Sect. Ser. 2*, 18: 1–297.
- . 1966. Remarks on the position, the delimitation and the subdivision of the Rubiaceae. *Acta Bot. Neerl.* 15: 1–33.
- Bremer, B. 1987. The sister group of the paleotropical tribe Argostemmateae: A redefined neotropical tribe Hamelieae (Rubiaceae. Rubioideae). *Cladistics* 3: 35–51.
- . 1992. Phylogeny of the Rubiaceae (Chiococceae) based on molecular and morphological data. *Ann. Missouri Bot. Gard.* 79: 380–387.
- & O. Eriksson. 1992. Evolution of fruit characters and dispersal modes in the tropical family Rubiaceae. *Biol. J. Linn. Soc.* 47: 79–95.
- & R. K. Jansen. 1991. Comparative restriction site mapping of chloroplast DNA implies new phylogenetic relationships within Rubiaceae. *Amer. J. Bot.* 78: 198–213.
- , K. Andreassen & D. Olsson. 1995. Subfamilial and tribal relationships in the Rubiaceae based on *rbcL* sequence data. *Ann. Missouri Bot. Gard.* 82: 383–397.
- Elias, T. S. 1976. A monograph of the genus *Hamelia* (Rubiaceae). *Mem. New York Bot. Gard.* 26: 81–144.
- Hemsley, W. B. 1879. *Diagnoses plantarum novarum mexicanarum*. Taylor & Francis, London.
- Lorence, D. H. 1990. A phylogenetic checklist of the genera of Rubiaceae in Mexico. *Acta Bot. Mex.* 12: 1–7.
- & J. D. Dwyer. 1988. A revision of *Deppea* (Rubiaceae). *Allertonia* 7: 389–436.
- Natali, A., J. Manen & F. Ehrendorfer. 1995. Phylogeny of the Rubiaceae–Rubioideae, in particular the tribe Tubieae: Evidence from a non-coding chloroplast DNA sequence. *Ann. Missouri Bot. Gard.* 82: 428–439.
- Robbrecht, E. 1988. Tropical woody Rubiaceae. *Opera Bot. Belg.* 1: 1–271.
- . 1993 [1994]. Supplement to the 1988 outline of the classification of the Rubiaceae, index to genera. *Opera Bot. Belg.* 6: 173–196.
- Schumann, K. 1891. Rubiaceae. *In*: A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien IV*. 4: 1–156. Wilhelm Engelmann, Leipzig.
- Standley, P. C. 1921. North American Flora: Rubiaceae. *Mem. New York Bot. Gard.* 32: 117–126.
- . 1930. Studies of American plants 4. *Field Mus. Nat. Hist., Bot. Ser.* 8(3): 153–154.
- Taylor, C. 1992. Revision of *Cosmibuena* (Rubiaceae). *Ann. Missouri Bot. Gard.* 79: 886–900.
- Verdcourt, B. 1958. Remarks on the classification of the Rubiaceae. *Bull. Jard. Bot. État* 28: 209–290.